



Central American climate and microrefugia: A view from the last interglacial

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ABSTRACT

The Last Interglacial (c. 128,000 to 115,000 years ago) was the last time when global temperatures may have been higher than those of the Holocene, but little is known about vegetation change or paleoclimate during that period in Central America. A new fossil pollen record from the lowland setting of El Valle, Panama, spanned the period from 137,000 to 98,000 years ago. We used multivariate analysis of modern and fossil pollen samples to provide the first regional quantification of Last Interglacial temperature and precipitation change and found mean annual temperatures were c. 1–2 °C warmer than modern, while precipitation was mostly similar to modern. The montane genus *Quercus* was intermittently present throughout the interglacial period, leading to the inference that this dispersal-limited taxon was surviving in microrefugia. Both charcoal and the early successional genus *Cecropia* were noticeably rare in the last interglacial compared with the Holocene. The modern absence of *Quercus* from Central Panama does not appear to be the product of interglacial warming, but rather a result of dry conditions in the late Holocene and human activity. It is suggested that humans greatly increased fire frequency, thereby favoring *Cecropia* and eliminating *Quercus* from the lower portion of its elevational range.

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1. Introduction

Nolan et al. (2018) identified a global pattern consisting of a 2 °C warming that initiated major change in both floral composition and structure between the end of the last ice age and the Holocene. A recent IPCC special report states that ongoing climate change will disrupt natural systems as pre-industrial temperatures are exceeded by 1.5 °C (<<http://www.ipcc.ch/report/sr15/>>). In both cases, the amount of temperature change to elicit a significant vegetation response is relatively modest.

A fundamental question exists as to whether the warming coming out of an ice-age, i.e. from a cold starting point, is

comparable with that of an already warm world (Colwell et al., 2008). In the cooler world, plants are close to the lower limit of their range of temperatures experienced in the last 2 million years of evolution, whereas today they are pressing close to the upper limit of that range. Obtaining an accurate modeled projection for vegetation change under future conditions is notoriously difficult, and even slight errors can lead to gross miscalculations of outcome (Cox et al., 2004; Huntingford et al., 2013; Rammig et al., 2010). An alternative is to look for analogous climates in the past and to determine the vegetation of those conditions. The closest analog that can be found to the projected conditions for AD 2040 described in the IPCC report is the Last Interglacial (LIG), c. 130–115 thousands of years ago (ka). At that time, because of orbital geometry (Imbrie et al., 1984), there was strong seasonality (Braconnot et al., 2012), an active El Niño Southern Oscillation ENSO (Hughen et al., 1999), and on average temperatures were about 2 °C above modern (Bakker et al., 2012; Harrison et al., 1995). As now, the polar warming of c. 3–4 °C (Epica-Community-Members, 2006) was more extreme than that of the tropics, which was estimated to have

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warmed by 1–2 °C (PAGES, 2016). While the LIG is not a perfect analog to our immediate future it contains two key ingredients: increased warming, and climatic instability.

The LIG, may have had multiple thermal peaks (Dutton et al., 2015), but most reconstructions find the warmest temperatures to have been c. 125 ka (PAGES, 2016). Very few high-resolution data are available for the LIG in the Neotropics. In the High Andes of Bolivia, striking aridity lowered lake level (D'Agostino et al., 2002) and induced a tipping point to dry, highly-seasonal systems (Bush et al., 2010; Hanselman et al., 2011). In the much wetter setting of the Colombian Andes, near modern conditions prevailed with no sign of strong aridity (Groot et al., 2011). Marine sedimentary records from the Galápagos Islands, Ecuador, and the Cariaco Basin, Venezuela, point to a northward migration of the inter-tropical convergence zone (ITCZ) during the interglacial (Lea et al., 2006; Riboulleau et al., 2014). A northward range expansion of the ITCZ should have brought more precipitation to lower Central America, and particularly to Panama. In the Atlantic rainforest of Brazil, the LIG supported a no-modern analog forest system (Ledru et al., 2009). No records exist for the influence of the LIG on lowland Central American systems.

Prior palynological assessments of glacial climates in Central America used the magnitude of the vertical range shift of taxa to quantify past cooling (Bush and Colinvaux, 1990; Bush et al., 1992; Correa-Metrio et al., 2012b, 2013; Islebe et al., 1995; Leyden et al., 1994). Especially in Panama, that signal of glacial-age cooling was heavily reliant on the interpretation of *Quercus* as a montane species that invaded lowland settings (Bush and Colinvaux, 1990; Bush et al., 1992; Piperno et al., 1991b). Observing a descent from a modern range that generally lies above 1500 m to 550 m–650 m elevation led to an inferred cooling of about 5–6 °C. Although this estimate aligned with other terrestrially-based estimates of cooling (Van't Veer and Hooghiemstra, 2000) and some coral studies (Guilderson et al., 1994), but was considerably greater than that of most models (CLIMAP, 1981; Cook and Vizy, 2006). Rather than relying on one or a few indicator species to quantify past climates, it would be preferable to generate transfer functions calculated from a broad suite of species found in modern analog samples (e.g. Huntley and Prentice, 1988; Peyron et al., 1998).

People arrived to the Americas in the deglacial period between 20,000 and 15,000 years ago (Dillehay et al., 2015). Hence, the entire Holocene period has been potentially altered by human activity. Indirect effects on vegetation, such as the extirpation of the megafauna (Metcalfe et al., 2016; Rozas-Davila et al., 2016) or changed fire regimes (Marlon et al., 2008; Power et al., 2010), could have shaped vegetation, altering what we perceive to be the natural state of systems. In the Americas, the LIG is the last time that there were near-modern temperatures, but that lacked a human presence. Consequently, studying the LIG provides unique insights into natural distributions of species and unmodified processes, such as fire periodicity.

Here we look at a long paleoecological record from El Valle, Central Panama, and compare it with an array of modern pollen assemblages from Panama and Costa Rica to draw inferences about the effect of warming on a highly diverse lowland tropical forest system.

1.1. El Valle revisited

The only record suggested to cover this interglacial from lower Central America is a low-resolution fossil pollen record from El Valle, Panama (Bush and Colinvaux, 1990). When that work was published, the lower section of the core was undated as it lay beyond ¹⁴C infinity. Subsequent U–Th dating (Table S1) has confirmed the base of the core included the glacial-interglacial-

glacial transition spanning marine isotope stages (MIS) 6–4. Bush and Colinvaux (1990) reported just six pollen samples for that period, but demonstrated the presence of mesic lowland or pre-montane forest similar to that of today. The strongest indicator of inferred climatic change during the last ice age was the presence of the montane taxon *Quercus*, which is currently found above c. 1500 m elevation, in lowland Panama. That *Quercus* was found in glacial-age samples was interpreted to indicate a cooling of c. 5 °C and the expansion of montane elements into the lowlands of Panama.

Shadik et al. (2017) described a fossil diatom sequence from a new core raised from El Valle in 2008. Using a combination of U–Th dating and comparison with directly dated isotopic records from speleothems they produced a chronology that is probably reliable ± 3 ka for the period from 137 to 98 ka. They observed the presence of a permanent lake throughout the period from c. 137 ka – 98 ka, i.e. from the termination of MIS 6, through MIS 5e and into MIS 5d. Somewhat drier conditions were suggested between c. 125 and 120 ka as the proportion of benthic diatoms increased, suggesting a shallower system. Here we present the fossil pollen record from the same core, capturing vegetation change across a glacial-interglacial transition from a premontane setting prior to human presence in the Americas.

We had two fundamental questions: 1) What was the temperature of the Last Interglacial in Panama? 2) What were the vegetational changes associated with the glacial-interglacial transition in the Panamanian lowlands?

2. Site description

The caldera of El Valle has a horseshoe-shaped rim that slopes upward to 1000 m away from the east-facing opening (Fig. 1). The flat floor of the volcano is about 3 km in diameter and lies at c. 590 m elevation. The climate of the El Valle region is humid tropical with temperatures ranging from 18° to 37 °C with a mean annual temperature (MAT) of 24.8 °C. Bioclim MAT data for this location is 24.2 °C, and as all other data used here draw upon the Bioclim data we accept 24.2 °C as the temperature of the crater bottom. The peaks surrounding El Valle range from 800 to 1040 m and, based on a –6 °C moist-air adiabatic lapse rate per 1000 m of ascent (Cavelier and Solis, 1996) would be expected to have mean annual temperatures of c. 22 °C. Mean annual precipitation (MAP) is c. 3000 mm (www.hidromet.com.pa) with a peak of rainfall between July and January, while the Bioclim MAP data for this location are about 2800 mm.

The caldera traps moisture from the prevailing easterlies so that, prior to human clearance, it would have supported premontane humid forest. Remnant forests in the caldera are found along streams and on the walls of the caldera above the modern town. These forests are rich in Gesneriaceae, Rubiaceae, Meliaceae, Sapotaceae, Myrtaceae and *Podocarpus*, but *Quercus* has not been collected from the area.

3. Methods

In 2008, a commercial water-well drilling truck, operated by veteran well-driller Mr. Richard Wharry, was used to retrieve a sediment core from the caldera floor of El Valle de Antón. The goal was to capture MIS5e and we report on the sediment raised between 43 m and 54 m depth below ground level. The 20 m-long core section contained three gaps where there was no core recovery, from 52.25 to 52.75 m (c. 128–126 ka), 50.3–50.8 m (c. 117–113 ka) and 46.2–45.7 m (c. 102–101 ka). These were probably sandy layers that offered no cohesion and caused the bottom of that core section to fall from the tube.

Cores were raised in PVC pipe, sealed in the field, and shipped to

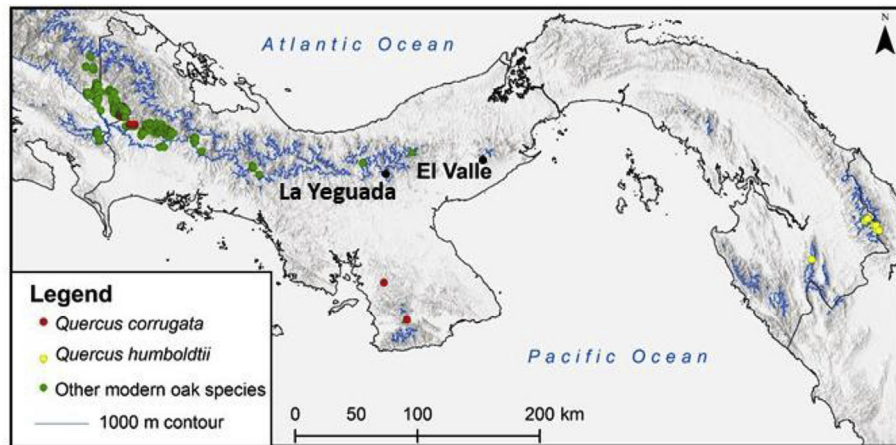


Fig. 1. Location of the El Valle caldera and La Yeguada. Collection data for Panamanian oaks, highlighting *Quercus corrugata* Hooker and *Q. humboldtii* Bonpl. relative to the 1000 m contour line. A more detailed map of the El Valle crater is available in Fig. S1.

the Florida Institute of Technology where they were stored in the dark at 4 °C. Upon opening, cores were described and subsampled for pollen, charcoal, and diatoms.

Pollen preparation followed standard protocols (Faegri and Iversen, 1989) with addition of exotic *Lycopodium* spores to facilitate calculation of pollen concentrations (Stockmarr, 1972). Pollen counts were made to a sum of 300 terrestrial pollen under a Nikon photomicroscope at x400 or, as needed, at x1000. Data were plotted in C2 (Juggins, 2003). Charcoal samples were gently disaggregated and filtered at 180 µm. The retained fraction was inspected at x20 using an Olympus photomicroscope and particles identified and quantified as mm² of charcoal per cm³ of sediment using ImageJ software (Clark and Patterson, 1997).

The modern and fossil pollen data were combined into a single matrix of 46 arboreal taxa and analyzed using Detrended Correspondence Analysis (DCA) (Hill, 1979). DCA scores-based distance among fossil samples, among modern samples, and between modern and fossil were summarized through kernel estimation of probability density functions (Wand, 2015).

The 46 arboreal taxa confidently identified in the fossil record have distributions representing a broad range of temperature and precipitation that can be modeled using bivariate kernel density estimates (Wand and Jones, 1995). For this purpose, we used 67 georeferenced pollen relative abundances of the same taxa from modern samples from Costa Rica and Panama (Bush, 2000). Mean annual temperature and precipitation from the sampled locations were used for building a bivariate probability density function (PDF) that describes pollen distribution along the environmental space defined by these two variables. Similarly, vegetation occurrences of the same taxa from the same countries were extracted from the BIEN database (Enquist et al., 2016) and summarized in an independent bivariate PDF. The credible distribution for each taxon was estimated by mixing pollen- and vegetation-based PDFs. For each fossil sample, the modeled environmental distributions of modern taxa were mixed proportionally to their relative abundance in the fossil assemblage, producing a probable environmental envelope for the represented time slice. The marginal distributions of temperature and precipitation were extracted from the highest 95% probability of the bivariate environmental space. Given that results strongly depend on taxa persistence through time (taxa that persist through time would flatten the climatic signal), the estimation was performed iteratively leaving from one to ten taxa out of the calculations each time. The final result corresponds to the inter-quartile range and mean of all possible solutions, constituting the

credible temperature and precipitation envelopes through time. Because we specifically wanted to investigate one of the 46 taxa, *Quercus*, we needed to ensure that it was not the primary driver of the observed patterns. Thus, a second environmental reconstruction was performed excluding *Quercus* from the pollen sum and the occurrence of all other taxa recalculated as percent non-*Quercus* arboreal pollen. All analyses were performed in R (R Development Core Team, 2018) especially package KernSmooth (Wand, 2015).

4. Results

4.1. Chronology

We adopt the recently published chronology (Shadik et al., 2017) that used ²³⁴U – ²³⁰Th to create the basic age-depth model for the 2008 El Valle core (hereafter EV08) (Table S1). Large errors were evident in the U–Th dates caused by detrital thorium in the lake sediment, such that only an approximate age model could be defined radiometrically. As was done with the deeper sediments from the Cariaco Basin, Shadik et al. (2017) refined the chronology through comparison with a directly dated compilation of Chinese cave data (Cheng et al., 2016) (See Fig. S2 for details).

4.2. Fossil pollen and charcoal

A CONISS zonation and description of pollen zones are provided in the supporting material (Fig. S3). The El Valle fossil pollen record was rich in arboreal types, with 46 taxa occurring in at least 5 samples and at > 2% of the pollen sum (Fig. 2). The percentage of forest pollen was consistently c. 50% of the pollen sum, with the remainder being Poaceae, Cyperaceae, and wetland taxa. An almost complete lack of charcoal with the exception of one peak at 100 ka, led to the Poaceae and Cyperaceae being treated as wetland species and expressed as percentage of total pollen, whereas other taxa are expressed as percentage of arboreal pollen (Fig. 2). Common arboreal types included Melastomataceae/Combretaceae with values ranging from 60% in samples from MIS 6 to as low as 20% at c. 112 ka. Similarly, Moraceae/Urticaceae pollen was abundant with between 20 and 40% of the pollen sum throughout. A broad assortment of forest species were represented with some taxa characteristic of modern montane forests e.g. *Quercus*, *Hedyosmum*, *Symplocos*, and *Podocarpus*, growing alongside *Acalypha*, *Alchornea*, *Apocynaceae*, *Ficus*, *Meliaceae*, *Psychotria*, *Sapotaceae*, *Urticaceae*/Moraceae, and *Zanthoxylum*, which typified lowland forest

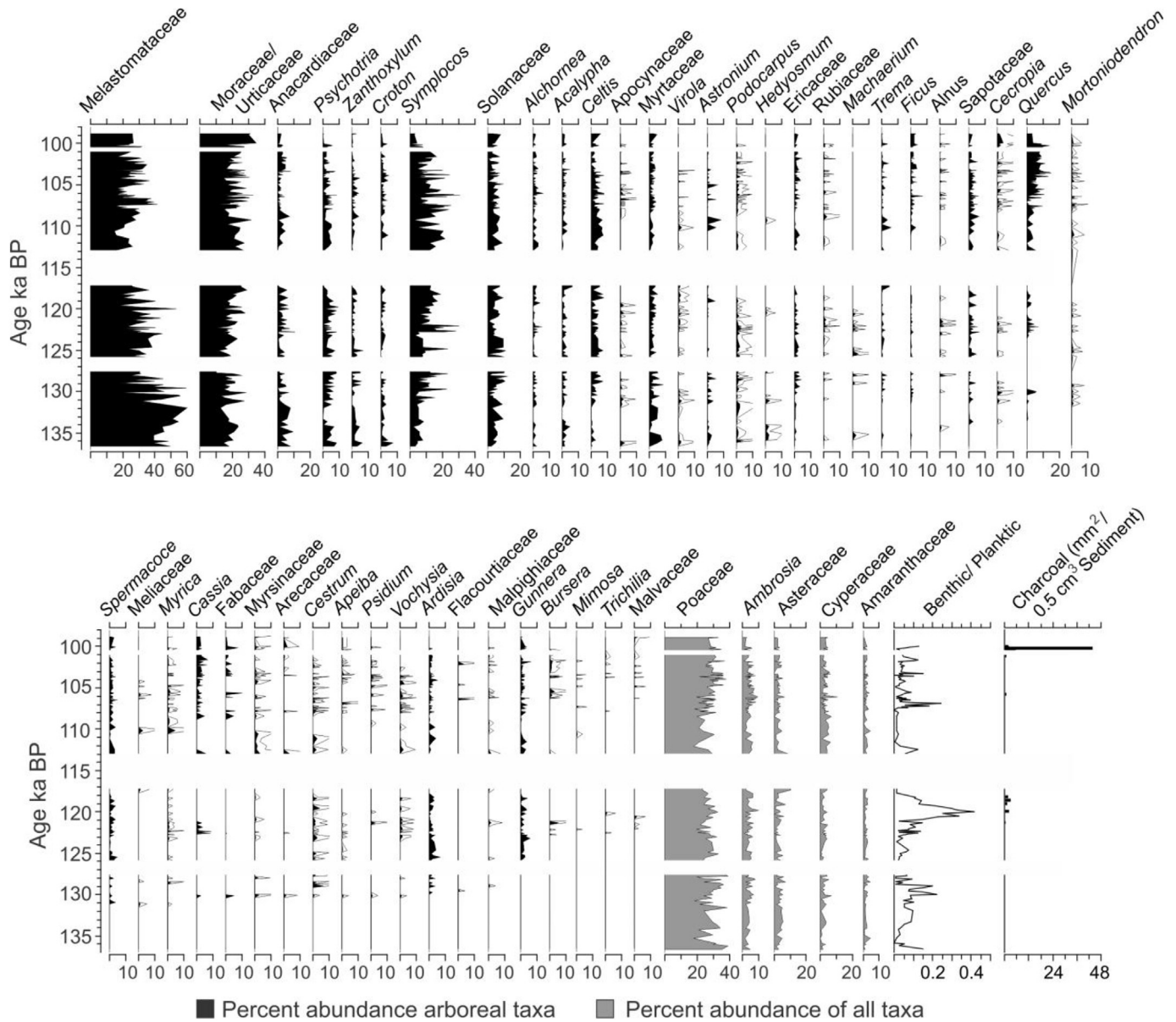


Fig. 2. Fossil pollen taxa from the crater lake of El Valle, Panama, with summary data for diatoms and charcoal. Arboreal species are expressed as % of arboreal pollen. Grasses and herbaceous taxa are expressed as % of total pollen. Open lines for pollen data represent 5x exaggeration. Benthic/Planktic is the ratio of diatom types (data from Shadik et al., 2017).

assemblages in other Central American studies (Bush, 1991, 2000; Correa-Metrio et al., 2011; Rodgers and Horn, 1996). *Cecropia* was notably scarce in the record, while *Quercus* was intermittently present throughout the record, and ranged in abundance from 0 to 12%.

Multivariate analyses (DCA) were run on a combined matrix of the arboreal pollen from El Valle and 68 previously published modern pollen samples (Bush, 2000). The modern samples were all drawn from mesic settings in Panama and Costa Rica (Table S2) and represented a range of mean annual temperatures from 7.5 to 26.5 °C (Fig. 3). The first two axes of the DCA that include *Quercus* (Fig. 3) produce a scatter of points in which the El Valle samples are clustered tightly, and provide a limited overlap of modern and fossil samples. The modern samples are structured from high to low temperature along DCA Axis 1, and the temperature of individual sites are shown as red (warm) to blue (cold) diamonds. Temperature isoclines are plotted based on the Bioclim defined

temperatures for the modern analog sites. The fossil samples are clustered (Fig. 3ab) so that fossil-to-fossil sample distances are all small, i.e. ecological similarity is high compared with distances between modern analog samples. The projected temperature for the fossil samples is in excess of 24 °C based on this analysis.

Because the fossil samples showed so little overlap and a tendency toward being no-analog systems, an alternative means was used to infer temperature and precipitation. Elaborating on a protocol used by (Bush et al., 2004), the environmental distribution of the 46 arboreal taxa in terms of mean annual precipitation (MAP) and mean annual temperature (MAT), produced a bivariate distribution for each taxon (Fig. S4). By using all records available for the species in the BIEN database (Enquist et al., 2016), the plot was close to a representation of their fundamental rather than realized niche. This niche space was weighted by fossil pollen abundances of individual taxon distributions to provide a paleoclimatic reconstruction (Fig. 4). The paleotemperature reconstruction suggested

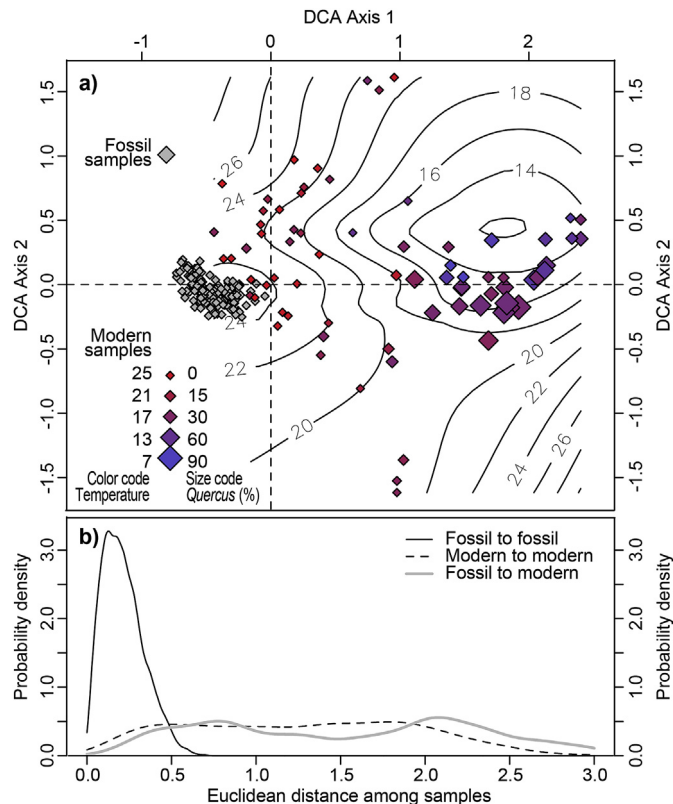


Fig. 3. Sample scores from the detrended correspondence analysis (DCA) of modern pollen assemblages from Panama and Costa Rica (Bush, 2000) and fossil pollen data from El Valle. Modern samples are color and size coded according to BIOCLIM (Hijmans, 2015) mean annual temperature (°C) values and *Quercus* percentage for each location, respectively. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

temperatures oscillated between c. 20 °C and 25 °C between 137 and 108 ka, with a distinct cooling trend between 108 and 98 ka where temperatures were projected to drop as low as 16 °C. The period with sustained warmest temperatures corresponded with the interval between 126 and 118 ka, when MAT reached as high as c. 25–26 °C. To determine the influence of *Quercus* on these estimates, a second analysis was run that excluded *Quercus* (Fig. 4). In this analysis the range of temperatures was more constrained, with no change to the warmer temperature reconstructions, but the cooling at the onset of the last glacial period was constrained to about 2 °C.

5. Discussion

The fossil pollen record of El Valle core EV08 had high, relatively stable proportions of Poaceae, Cyperaceae and Asteraceae (Fig. 2). While these taxa can be found in any setting, their abundance in this record combined with the absence of regular charcoal occurrence suggests the presence of a marsh surrounding a shallow lake, rather than an upland grassland. This inference is consistent with the diatom record from the same core, which indicates an open-water setting between c. 137 ka to 98 ka. The diatom data suggest somewhat drier conditions or a change to water inflow regimes between 125 and 120 ka. That this oscillation is not evident in the pollen data suggests that although influencing local hydrology, this dry event does not significantly affect forest structure or composition. Fire is very rare in this setting, with only one certain fire event at 99 ka and one, perhaps two, lesser events at c. 120–119 ka (Fig. 2).

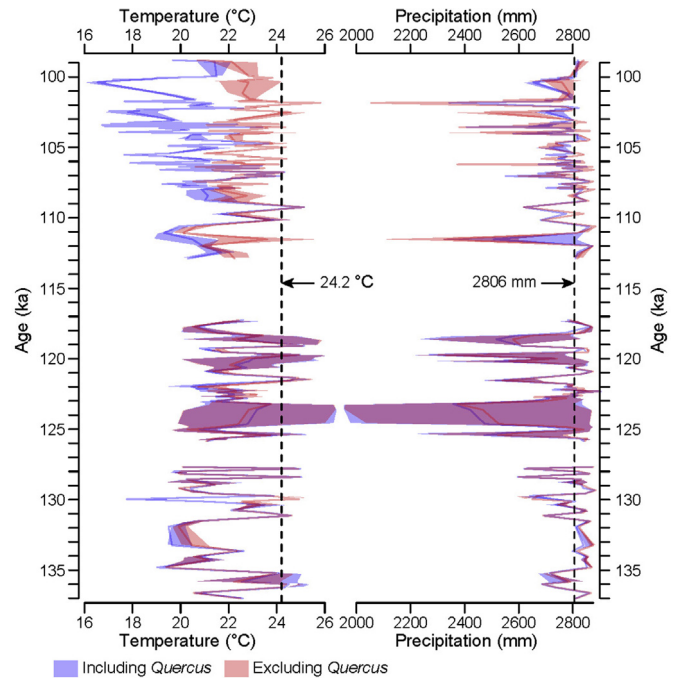


Fig. 4. Mean annual temperature (a) and precipitation (b) reconstructions for El Valle, Panama, for the period 137 to 98 ka. a) Two temperature estimates are shown calculated on 46 arboreal taxa that included *Quercus*, and 45 arboreal taxa that excluded *Quercus* from the dataset. The 95% confidence interval is shown as shaded blue (with oak) or pink (without oak) and purple where they overlap. The lines represent the mean value of the reconstruction for mean annual temperature. The black dashed line represents the modern Bioclim estimate of 24.2 °C for the crater floor of El Valle. b) Reconstructed precipitation showing the 95% confidence interval and mean value for mean annual precipitation. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

The most important finding about this system is that despite the climatic changes associated with the glacial-interglacial cycle, forests were always present adjacent to El Valle. Melastomataceae was the most abundant woody pollen type, especially near the base of the core, was associated with moist lowland forest (Punyaseena et al., 2008) and, in combination with Urticaceae-Moraceae, probably also indicated significant gap formation or disturbance (Denslow, 1987). Other taxa in the record represented a blend of lowland, premontane and montane plants. *Symplocos* which is strikingly abundant in this record is a small tree usually found between 1300 and 3300 m elevation in Panama (Kelly and Almeda, 2002; Woodson et al., 1976). Other taxa, such as Apocynaceae, can grow in lower montane forests, but their pollen is far more abundant in settings <1000 m elevation (Bush, 2000; Grabandt, 1985; Rodgers and Horn, 1996).

The multivariate analysis of the El Valle fossil samples provided a tight cluster with few modern analog samples overlapping them in ordination space. This outcome suggested that fossil samples were largely without modern analog. That they clustered so tightly when the main gradient on Axis 1 was temperature, suggested that if they responded to temperature change it was not in the same way that is exhibited by modern samples.

The environmental modeling provided an inferred temperature range of c. 16–26 °C within the period from 137–97 ka, representing a warming of about 1–2 °C above the modern temperature of 24.2 °C and a cooling of almost 8 °C early in the last interglacial. While the warming was consistent with other estimates of c. 2 °C warmer than modern conditions in the LIG (Groot et al., 2011; Hanselman et al., 2011), the cooling trend at the onset of the last ice

age appeared exaggerated, but we will return to this later. Precipitation was similar or even slightly wetter than modern, although there were periods of lowered rainfall centered on 126–118 ka. While we do not believe that the precipitation data based on arboreal pollen should be taken too literally, the data do suggest that the LIG was a time of increased variability in precipitation with a propensity toward drought. These data are broadly consistent with fossil diatom data from this core, which were interpreted to indicate a shallower lake system, reduced rainfall, and less inwash of benthic diatoms between c. 125 and 120 ka (Shadik et al., 2017). Analysis of fossil corals from the Caribbean island of Bonaire projected a c. 3 °C warming relative to pre-industrial temperatures and increased strength or length of the dry season centered on 125 ka (Brocas et al., 2016); data that are consistent with our findings. It is important to note that the period when *Quercus* was missing from the El Valle record overlaps with this period of heightened soil moisture deficits.

There were two other observations of note arising from this record. The first was the paucity of fire events recorded at El Valle. In the 30,000-year El Valle record, which included an interglacial and a transition to glacial conditions, only two fires were documented. These data were a marked contrast to the Holocene histories of Central American paleoecological records that all exhibited frequent fire occurrences (Behling, 2000; Bush and Colinvaux, 1994; Bush et al., 2016; Horn and Kappelle, 2009; Horn and Sanford, 1992; Kennedy and Horn, 1997) but consistent with data for very little fire activity from mid-elevation Mexican lowland Guatemalan forests in the last glacial (Correa-Metrio et al., 2012a; Domínguez-Vázquez et al., 2018). Regularly occurring fire in these mesic landscapes appears to be a sure sign of human activity. The second finding was that *Cecropia*, an early successional tree that commonly accounts for 20–50% of the pollen sum in premontane forests, was rare in MIS 5e at El Valle and never exceeded 3% of arboreal pollen in any sample. The abundance of Melastomataceae indicated forest disturbance, but the rarity of *Cecropia* suggested that the forest was so dry that *Cecropia* was not favored or that the disturbance gaps were small (Brokaw, 1985; Pearson et al., 2003). We raise a hypothesis to be tested in future studies that *Cecropia*, at least in such premontane settings, has benefited from human-style forest disturbance and became a far more widespread tree of regenerating forest in human-influenced landscapes than in truly natural settings.

5.1. Current and past ecology of *Quercus*

The center of *Quercus* diversity is in Mexico, where about 160–165 species occupy a wide range of habitats (Nixon, 2006). In Central America, *Quercus* can occur from sea-level to about 3300 m elevation (Kappelle, 2006), but as the species diversity falls along the Isthmus of Panama the modern range becomes more restricted. The southernmost of the lowland oaks, *Q. oleoides*, is restricted to dry forests between Mexico and northern Costa Rica (Boucher, 1983). In Panama, 12 species of *Quercus* grow, all of which are restricted to humid montane settings (Nixon, 2006), often co-occurring with species such as *Ulmus*, *Ahnus*, *Myrica*, *Gunnera*, *Symplocos*, Melastomataceae and Ericaceae, and the understory bamboo *Chusquea*. The distribution of oaks follows the mountain spine of lower Central America. In general, oaks occupy niches with MATs of 7.5–22 °C (Fig. 5a). One of these oaks, *Q. corrugata* Hooker, has a thermally and geographically disjunct population that grows at c. 380–440 masl in the Azuero Peninsula, Panama (Fig. 1). This population is the lowest growing oak in Panama (Fig. 5a), surviving the warmest temperatures (MAT 24.6 °C), and even this population appears as a bimodal hump that is quite different from the main distribution of the species (Fig. 5a). The twelfth species,

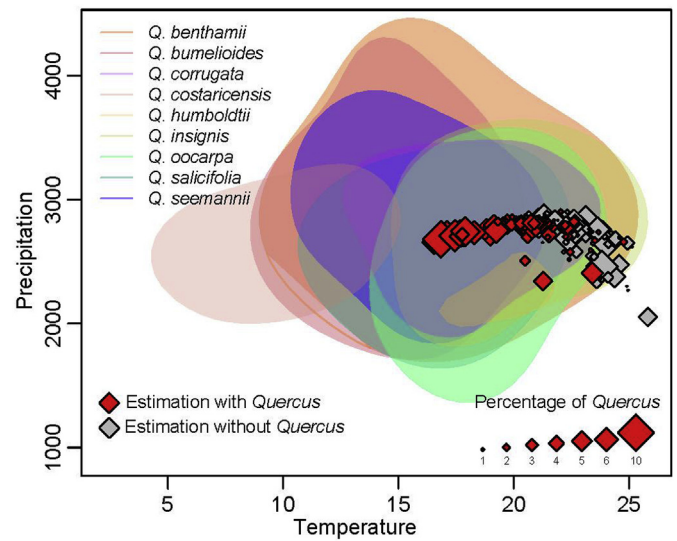


Fig. 5. Bivariate environmental envelopes for the 10 species of *Quercus* with more than 10 records from Panama and Costa Rica in the BIEN database. Red diamonds represent the inferred growing conditions if *Quercus* is included in the analysis. Gray diamonds when *Quercus* was excluded from the reconstruction. Temperature is MAT °C, Precipitation is MAP mm. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

Q. humboldtii, is the only one that grows to the west of the lowland plain of Central Panama, and is endemic to the Darién (c. 310 km from El Valle) and Colombia. Thus, a 600 km-wide saddle of lowlands in Central Panama interrupts the distribution of oaks. *Quercus*, almost certainly *Q. humboldtii* or its ancestor, arrived in Colombia about 450 ka, and during its migration eastward it could have been the oak to colonize the most disjunct hilltops of Central Panama. *Q. humboldtii* requires moist conditions, and commonly grows in areas receiving >2000 mm of precipitation per year. This tree grows across a wide elevational range from 3300 m down to c. 1000 m (Fernandez-M and Sork, 2007), with an upper thermal limit of c. 24 °C mean annual temperature (Orwa et al., 2009).

That only one oak successfully crossed the lowland landbridge, and that gene flow was so rare that an endemic species emerged in the Darién (Gentry, 1977), suggested that oaks were probably dispersal limited even before the loss of megafauna. Genetic analysis of Isthmian oaks revealed a complex history both of speciation and of divergence presumably arising from barriers to distribution. Even the relatively narrow Isthmus of Tehuantepec, which forms a c. 65 km wide gap between peaks >1000 m in Mexico, apparently split *Quercus* populations such that they evolved distinctive genetic traits on either side of the divide (Rodríguez-Correa et al., 2017). In a study comparing a pair of Costa Rican oak species, the upper montane oak, *Q. costaricensis*, showed strong phylogeographic structure suggesting limited connectivity through time, whereas the lower montane *Q. bumelioides* exhibited no such pattern, suggesting Pleistocene or Holocene population connectivity along a mountain range (Rodríguez-Correa et al., 2018). These data reinforced that *Quercus* dispersal was primarily reliant on gravity, with relatively weak transport by animals (Nixon, 2006).

Fossil pollen records from La Yeguada (Bush et al., 1992) and El Valle, Panama (Bush and Colinvaux, 1990), both revealed oak as a component of ice-age forests at c. 600–1000 m elevation in Central Panama. To occupy these settings, oaks would have required a substantial downslope population expansion and dispersal across intervening lowlands to reach the isolated peaks around El Valle.

Quercus was not recorded in the oldest samples from El Valle, appeared briefly between 130 and 128 ka, disappeared temporarily

between c. 128 and 125 ka, but returned to the record thereafter. For a taxon that appeared to have limited dispersal capacity, it was very unlikely that each disappearance of *Quercus* from the pollen record documented a true extinction, and each occurrence a new immigration. Far more probable was that *Quercus* populations were locally maintained, but fell below the threshold of detection when populations were restricted to small settings further from the lake (Fig. 6a).

In modern systems where *Quercus* occurs, it is frequently the dominant species (Nixon, 2006) and this is reflected in its pollen abundance. Thus, *Quercus* pollen is often present at values > 40% or absent from samples. It is unusual to find *Quercus* at 3–10% of the pollen sum in mesic lowland or premontane assemblages (Bush, 2000; Correa-Metrio et al., 2011; Rodgers and Horn, 1996). That *Quercus* was generally found at this lower abundance at El Valle pointed to a system where oak was not a dominant taxon in forests beside the lake. *Quercus* populations probably existed in microrefugia (sensu McGlone and Clark, 2005) slightly upslope of the lake, but within the caldera.

As a thought experiment, let us assume that *Quercus* was present during the LIG in the upper half of the slopes of the caldera, i.e. above 740 m elevation. How much would this downslope expansion affect the area occupied by *Quercus*? Because of steep slopes throughout the elevation range between 500 m and 1000 m throughout Panama, the answer is that the range of *Quercus* would have been negligibly larger (Fig. 6b). Consequently, the barriers to oak migration were still present.

Between c. 120 and 100 ka, *Quercus* pollen increased in abundance at El Valle as conditions cooled and expanding populations of oaks migrated downslope. It is important to re-iterate that although mean annual temperature (22 °C) and precipitation (>2000 mm) on the peaks around El Valle appear suitable for *Quercus* growth today (Figs. 1 and 8 ab), none has ever been

documented there (orange highlighted area in Fig. 6c).

From the paleoecological records, we find that *Quercus* occurs more frequently at lower elevations during interglacial conditions, than is currently observed today. As only one *Quercus* species occurs in eastern Panama, crossing the central lowlands may only have happened once. Paleoecological data suggest that *Q. humboldtii* or its progenitor, spread out of Panama and into the Colombian Andes about 478 ka (Van't Veer and Hooghiemstra, 2000). For oaks to cross the lowlands of Panama is clearly a rare event, and it is probable that the hilltops in Central Panama were important stepping-stones in that migration. Given this rarity, the *Quercus* documented in the Last Interglacial and Glacial at El Valle (590–1000 masl) and in the Late Glacial at La Yeguada (650 masl) (Bush et al., 1992), may have been remnant microrefugial populations of that earlier migration.

The role of microrefugia in facilitating population survival under adverse conditions (Collins et al., 2013; Rull, 2009) and rapid expansions as conditions become more favorable (Cheddadi et al., 2017) is increasingly recognized. Indeed, to obtain plausible migrational velocities, microrefugia need to be invoked in settings ranging from the tropical lowlands (Correa-Metrio et al., 2013) to the boreal fringe (Birks and Willis, 2008; McLachlan and Clark, 2005). In the context of Panamanian hilltops, the microrefugia could have formed a single continuous population in the uplands around El Valle as conditions cooled and allowed *Quercus* to move downslope. This population would still have been isolated from those in Chiriqui because of the low elevation of the intervening area. The disjunction of the El Valle oaks would have become more extreme in the warmest conditions, as only the wettest, highest, hilltops would have been likely to have supported microrefugia, causing fragmentation into small metapopulations (Mosblech et al., 2011).

At La Yeguada (650 m elevation; MAT 23.2 °C), *Quercus* survived into the Holocene until about 4000 years ago (Bush et al., 1992), and

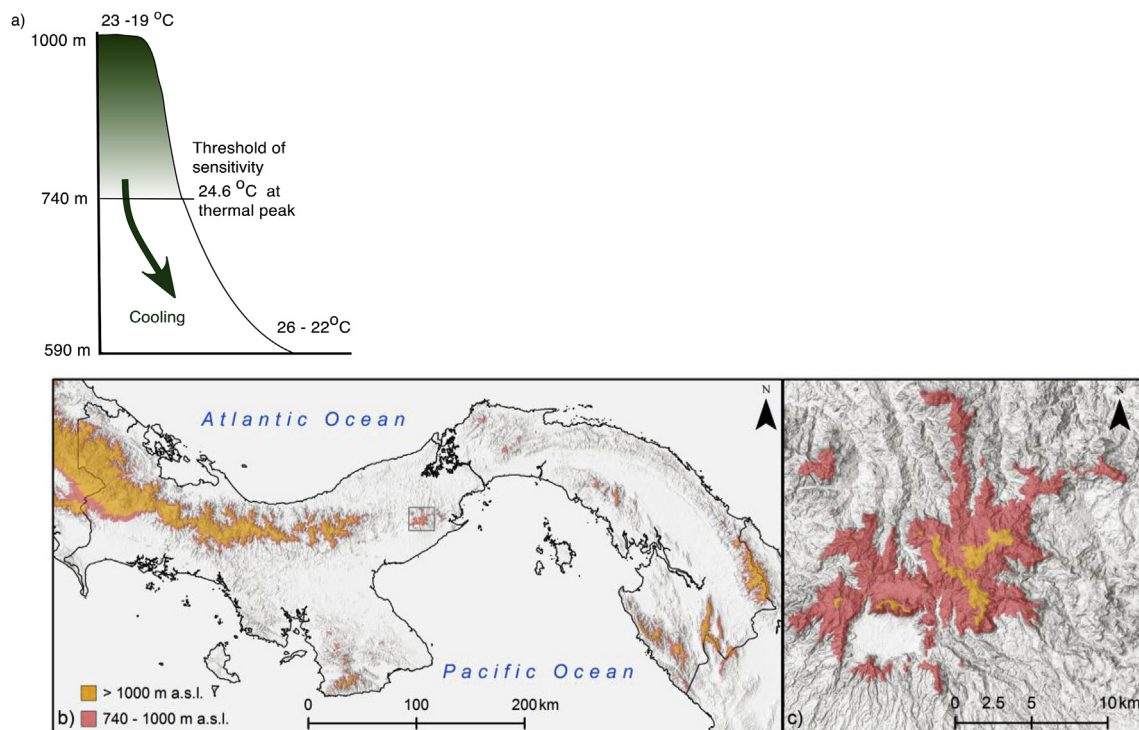


Fig. 6. Schematic diagram showing the relative position of *Quercus* populations at the peak of MIS5e relative to elevation. The orange represents modern settings above 1000 m that should be capable of supporting *Quercus* based on the modern occurrence of the majority of Panamanian species in western Panama. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

at El Valle it also grew during warmer-than-modern temperatures in MIS 5e and in the Pleistocene/Holocene transition (its Holocene history in El Valle is unknown). The apparent loss of these populations as late as 4000 years ago coincides with two changes. The first was a transition toward drier climates in the late Holocene (Haug et al., 2001), and the second was the widespread expansion of human activity in Panama (Cooke, 2005; Piperno et al., 1991a). Both of these factors could have played a role in reducing *Quercus* coverage. The drying could have caused cloudbase to lift (Anchukaitis and Evans, 2010), and even if the forest could survive the new conditions, it may not have been able to regenerate once cleared (sensu Sternberg, 2001). The foothills and premontane habitats were widely used by humans, and even areas that we think of as being remote and uninhabited had millennia of use and occupation (Bush and Colinvaux, 1994). It seems likely that coupled climate change and human activity through felling or fire management eroded the downslope range of *Quercus*, leaving us with a shifted baseline (sensu Pauly, 1995) of expected occurrence. We infer that mesic forests of *Quercus* persisted as microrefugia on isolated hilltops throughout the Last Interglacial and glacial period, and that its elevational distribution has been truncated by human activity. As MIS5e was the most extreme Quaternary interglacial (Lisiecki and Raymo, 2007), and *Quercus* survived it around El Valle, it is very likely that these hilltop populations were continuous features of the landscape since the initial migration that resulted in *Q. humboldtii* establishing in the northern Andes.

This realization that we are missing the lower limit of *Quercus* distributions, does not affect our reconstructions of when it is too warm for *Quercus* to occur, but it would influence the degree of inferred cooling as *Quercus* appears in the record. Rather than using the temperature reconstructions that include *Quercus*, it would be prudent to exclude it from the analysis to avoid potential bias. By removing *Quercus* from the modeling, the temperature reconstruction for the warmest period (where *Quercus* pollen was absent) is unchanged, but the strong cooling inferred for the onset of glaciation is greatly reduced (Fig. 4). The flatter temperature response still has a 1–2 °C warming relative to modern, but cooling is now only about 2 °C and that cooling occurs further into the glacial period; both the amount and the timing of cooling providing a more credible reconstruction than when *Quercus* is included (Fig. 4a).

Beyond realizing that some assumed biogeographic patterns are probably products of human activity, these data also provide a note of caution regarding paleoclimatic interpretations of glacial temperatures in Panama. Our interpretation of a c. 5 °C cooling at the last glacial maximum (Bush and Colinvaux, 1990; Bush et al., 1992) relied heavily on the occurrence of oaks c. 800–1000 m below their common range limit. This estimate exceeded many temperature reconstructions based on general circulation models, which were usually about 2–3 °C (Braconnot et al., 2012). While other terrestrial records at other elevations support a c. 5 °C cooling (Hooghiemstra et al., 1992; Martin, 1964), the data we present here mean that it would be wise to look for a broad array of taxa to develop the next estimates of glacial paleotemperature from the Isthmian lowlands.

6. Conclusions

Marine Isotope Stage 5e was about 1.3 °C warmer-than-modern in the Central Panamanian lowlands. Conditions favored the continuous existence of forest, a marsh, and a shallow lake. No evidence is found of the severe interglacial drought documented at Lake Titicaca in Bolivia, and precipitation was generally similar to current conditions. A dry event is documented between 125 and 120 ka, when lake level fell. At El Valle, premontane and lower

montane forest elements coexisted throughout the interglacial with some species, such as *Quercus*, probably surviving in microrefugia. *Quercus* appears to have survived numerous prior interglacials only to be lost from Central Panama within the Holocene. We suggest that a combination of late Holocene drying and human clearance of premontane forests may have truncated the vertical distribution of *Quercus* especially on the isolated hilltops of Central Panama. We urge caution in over-reliance on *Quercus* occurrence to quantify past cooling, and recommend using a broad swath of species. Two other findings are that fire was extremely rare in this record, contrasting markedly with Holocene patterns from elsewhere in Panama. We conclude that humans have caused the great majority of those Holocene fires, and that regular fire activity is a sure sign of human activity in these forest systems. Lastly, that another human indicator may be the early successional genus, *Cecropia*, whose pollen was surprisingly rare in last interglacial sediments compared with modern systems.

We find that the lowland forests of Panama are likely to be resilient to change at least until conditions warm past those experienced in the LIG. The role that humans play in deforestation, climate change through deforestation, and through burning are far more likely to cause a collapse of rainforest systems than climate change. We see this with cautious optimism for, while controlling warming does not lie within the power of any one country, controlling deforestation through human action does.

CRediT authorship contribution statement

G.M. Cárdenes-Sandí: Data curation, Investigation, Writing - original draft. **C.R. Shadik:** Data curation, Investigation, Writing - original draft, Formal analysis. **A. Correa-Metrio:** Formal analysis. **W.D. Gosling:** Writing - original draft. **R. Cheddadi:** Writing - original draft. **M.B. Bush:** Writing - original draft.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.quascirev.2018.12.021>.

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